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Seasonal dynamics of the abundance of Bothriocephalus opsariichthydis (Cestoda, Pseudophyllidea) and differential infection of carp fingerlings of different genotypes

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SUMMARY

Investigations conducted during two seasons on one summer old carps have shown that the summer distribution of bothriocephalids corresponds to Poisson distribution while in autumn the parasites decrease in number and their distribution acquires an overdispersed form. The conducted crossings have made possible the determination of the role of hereditary factor in the variability of fishes on the infection with bothriocephalids. In summer when the distribution of parasites corresponded to Poisson distribution no differences in the infection of fishes with bothriocephalids of different genotypes were observed. In autumn, with an overdispersed form of distribution such differences took place. This fact proves that the initial infection, in July, is of non-selective character and in autumn changes for differential one.

The type of distribution of parasites within host populations provides important information on the nature of host-parasite relations. When parasite population follows the Poisson distribution, uniform probability of infection and uniform resistance to infection among individuals

of the host population can be assumed to prevail (Breev, 1972). The other type, overdispersion, is more common; its main characteristic is the unequal probability of infection of hosts, and, consequently, non-uniform individual susceptibility to infection (Kennedy, 1958). Studies with silver carp infected with the cestode Digramma interrupta have shown the unequal distribution of parasites in fish of different age groups. In fish up to 2 years of age the cestodes were distributed according to the Poisson series, while in older fish there was overdispersed distribution (Breev, 1972). Similar results were obtained with cisco [Coregonus sp. (Tr.)] infected with the cestode Proteocephalus exiguus (Anikieva and Malakhova, 1982). It should be noted that in these two cases the infection rate decreased with the age of the host, while, on the contrary, the number of parasites per host (infection intensity) increased with the age of the host. Possibly, a non-selective infection pattern becomes selective (differential) with the age of the host, and this may be determined to some extent by genetic differences between the members of the host population.

Currently the genetic constitution of individuals can be determined by means of biochemical gene marker protein electrophoresis (Altukhov, 1983). This method can evaluate the effect of the host's genetic constitution on susceptibility to infection with the parasite, and demonstrate that the transition from Poisson to overdispersed distribution is related to differential infection of the host.

The aim of this research was first, to study the seasonal distribution of the cestode Bothriocephalus opsariichthydis in carp populations during the first year of the life of the fish, second, to determine the part played by the inherited variability of fish with respect to the susceptibility to infection with this parasite, and third, to reveal the differences in the infection with this parasite of different carp genotypes in relation to seasons.

Materials and Methods

At the end of May 1985 5000 carp larvae, obtained as a result of artificial fertilization of eggs from one female by the sperm of two males, were released into a pond at the Nemeshaev State Farm Technical School in the Kiev Region, where they were reared on natural feed until the end of October. During this period 3 carp samplings were taken, each on the average consisting of 200 fish. In 1986 di-allele crossing of 2 females and 2 males was performed. As a result, four progenies were obtained from individual crossings. Ten thousand larvae from each progeny were released into each of four identical ponds. These ponds had identical areas, a common water supply system and were directly adjacent to each other. In August 100 fish were removed from each pond, and additionally, 200 fish at the end of October, except from crossing No. 4. Dissection and post-mortem examinations were done according to accepted ichtyopathological methods (Bykhovskaya-Pavlovskaya, 1985).

For electrophoresis, blood, and liver and muscle suspensions from each fish were used. Transferrin (Tf) types were determined in blood serum, esterases (Est-2) in the muscles, and lactatedehydrogenases (LDH-C1,C2) in the liver.

Separation of serum proteins and esterases was done by the disc electrophoresis method (Davis, 1964); separation of lactatedehydrogenase was done in tris-EDTA-borate buffer (Peacock et al., 1965) in 7.5% acrylamide gel. Gels were stained according to established methods (Salamenkova and Malinina, 1976).

Results

The distribution of Bothriocephalus in the examined carp populations was found to be season-related. In 1985 the highest infection rates and the lowest infection intensity (number of parasites per host) were noted in the month of July. The situation changed in October, such that the infection rate (the number of infected fish) became reduced by more than half, while the infection intensity increased (Table 1). In July and August juvenile fish were frequently encountered alongside sexually-mature fish, while in October there were only sexually-mature ones. In July Bothriocephalus distribution corresponded closely to the Poisson series, while as early as in August a clear tendency towards overdispersion became apparent; in October the overdispersed distribution was clearly evident.

Table 1
Bothriocephalus infection in carp figerlings in 1985

Month	IR %	II	M	σ^2	χ^2	d.f.	n
July	41	1.32	0.54	0.55	0.89	2	189
August	28	1.67	0.54	1.12	33.09 *	2	232
October	14	2.87	0.43	12.89	54.49 *	2	220

Note. Here and in Table 2: IR - infection rate; I I - infection intensity; M - mean infection; σ^2 - fish dispersion according to infection; χ^2 - values of ratios between expected and observed distributions of the parasites; d.f. - degrees of freedom.

Asterisks mark data where differences are statistically significant at $p < 0.001$.

Table 2
Bothriocephalus infection in carp fingerlings in 1986

Crossing	Month	IR %	I I	M	σ^2	χ^2	d. f.	n
1×1	August	59	1.87	0.78	1.39	16.43 **	3	110
	October	8	1.57	0.20	0.23	8.30 *	2	184
2×2	August	20	1.40	0.28	0.50	1.74	2	102
	October	15	2.11	0.31	0.91	33.61 **	2	182
2×1	August	70	1.88	1.32	1.80	4.66	5	105
	October	23	3.10	0.71	2.36	132.65 **	3	182
2×2	August	62	5.48	3.40	17.96	143.52 **	7	101

Note. * - mark data where differences are statistically significant at $p < 0.05$;
** - significance at $p < 0.001$.

In August 1986 in two of the four ponds the parasite population followed the Poisson distribution, and in the other two ponds it was overdispersed (Table 2). However, in October in the three carp samplings examined the parasite distribution was overdispersed. Thus, during the first year of life of the fish populations there occurred a change in the number of parasites and in the type of their distribution. In July and August the parasites became distributed non-selectively with respect to the hosts. During this period the parasite distribution was of the Poisson type, but in the autumn it became overdispersed.

The results obtained in 1986 have shown that the degree of infection of fish with Bothriocephalus in different ponds under identical conditions could differ (Table 2). Two-factor dispersion analysis has permitted the evaluation of the type of crossing [of fish - Tr.] in determining the parental effect on the variability of susceptibility of the progeny to mean infection. The results of this analysis

have demonstrated the part played by the resulting inherited variability of fish with respect to Bothriocephalus infection. The overall share of the parental effect constituted 0.16 ± 0.006, maternal 0.10 ± 0.002 and paternal 0.014 ± 0.002. Thus the infection of carp with Bothriocephalus was seen to depend to a certain extent on hereditary factors. However, they accounted for only 16% of the total variability of fish with respect to this index.

In 1985 polymorphism of three loci, transferrins, serum esterase and liver lactatedehydrogenase, was observed in the fish examined. In addition the type of scale cover was also used as a genetic marker; the type of scale covering is under the control of the locus which determines the development of the scattered scale type following homozygous combination of recessive alleles (Kirpichnikov, 1979). A comparison of the infection rates in fish of different genotypes has revealed a difference between them in two loci in the month of October - Tf (transferrins) and Est-2 (esterase-2). The high infection rate in fish genotypes AA and BC according to the Tf locus was significantly lower than in AC heterozygotes, and carp genotype AB harbored no parasites at all (Table 3). The effect of genotypic variability according to the Tf locus on Bothriocephalus infection in carp in July constituted only a very small portion (h^2=0.002; $p > 0.05$), in August the portion became somewhat greater but not statistically

significant (η^2=0.01; $p > 0.05$), and only in October it became statistically significant (η^2=0.07; $p < 0.001$). Differences between the SS and SF genotypes according to the Est-2 locus with respect to Bothriocephalus infection were statistically significant only in October (F_ϕ =4.5; $p < 0.05$), while differences between genotype loci LDH-C and the type of scale covering were inapparent throughout the entire season (Table 3).

Table 3 51/
Portion of fish ($q \pm m$) of different genotype loci of transferrin (Tf) and serum esterase (Est-2) infected with Bothriocephalus in the summer and autumn of 1985

Month	Tf							
	AA		AB		BC		AC	
	$q \pm m$	n	$q \pm m$	n	$q \pm m$	n	$q \pm m$	n
July	0.43±0.04	140	0.40±0.13	15	0.40±0.22	5	0.36±0.11	19
August	0.28±0.04	145	0.33±0.10	26	0.54±0.14	17	0.30±0.10	24
October	0.18±0.03	135	0.00	21	0.33±0.14	12	0.04±0.04	24

	Est-2					
	SS		SF		FF	
	$q \pm m$	n	$q \pm m$	n	$q \pm m$	n
July	0.43±0.10	23	0.45±0.05	101	0.35±0.06	55
August	0.20±0.13	10	0.29±0.04	109	0.28±0.06	83
October	0.33±0.11	18	0.12±0.03	111	0.16±0.04	89

Note. AA, AB, BC and AC - genotypes of the Tf locus; SS, SF and FF - genotypes of the Est-2 locus.

In 1986 there were three polymorphic loci among the fish examined:Tf, LDH-C1,C2 and in two crossings about half the number of fish had scattered type of scale covering. In August there were no significant differences between the fish of different genotypes (Table 4). In the autumn significant differences were noted between genotypes of LDH-C1 locus in the crossing No. 3. There were fewer infected fish among the heterozygous genotypes CC1 than among CC homozygotes

(t=2.03; $p < 0.05$). The effect of genotype loci LDH-C1 in this crossing was not significant during August ($h^2 = 0.005$, $p > 0.05$), but in October it rose to become statistically significant ($h^2 = 0.02$; $p < 0.05$).

Thus, differences between fish of different genotypes in the degree of bothriocephalosis infection occurred only at the end of October when the parasite distribution was overdispersed; no differences could be discerned in the summer.

Table 4
Portion of fish of different genotype loci of transferrin (Tf), liver lactatedehydrogenase (LDH-C_1,C_2) and type of scale covering in the summer and autumn of 1986

Month	Tf		LDH-C_1,C_2			Scales type	
	AA	AB	C_1C_1	C_1C_1	$C_1C_1C_2C_2$		
August				0.42±0.07	0.46±0.07	0.47±0.06	0.31±0.08
				53	46	75	36
October	0.11±0.03	0.04±0.02		0.08±0.03	0.07±0.03	0.06±0.02	0.12±0.05
	97	79		87	91	132	52
August		0.20±0.04		0.21±0.06	0.21±0.06	0.15±0.05	0.26±0.07
		102		43	47	60	42
October		0.15±0.03		0.16±0.04	0.13±0.03	0.14±0.03	0.16±0.04
		182		74	104	102	80
August	0.68±0.06	0.75±0.06	0.72±0.07	0.75±0.06			0.70±0.04
	53	51	47	55			105
October	0.21±0.04	0.21±0.04	0.30±0.05*	0.17±0.04*			0.23±0.03
	84	92	83	99			182
August		0.68±0.05	0.71±0.06	0.61±0.08			0.68±0.05
		101	51	41			101

Note. AA, AB - genotypes of the Tf locus;
C_1C_1, C_1C_1, $C_1C_1C_2C_2$ - genotypes of the LDH-C_1,C_2 locus;
* - statistical significance at $p < 0.05$

Changes in the distribution of Bothriocephalus 52/ in carp populations have been observed during the first year of life of the fish. In the summer there was high infection

rate and relatively low intensity of infection, while in the autumn the proportion of infected fish sharply declined, and the mean number of parasites per infected fish increased. In the summer the parasite distribution approached Poisson distribution, while in the autumn it was overdispersed. Clearly, the host fish population could be divided into 2 groups. One group became free of parasites and the other became additionally infected. There is reason to believe that this pattern was determined by the biological diversity of the host population and individual resistance to infection which, as shown by the experimental crossings, was, to a certain extent, controlled genetically. In fact, the share of the heredity factor in the total variability of fish with respect to Bothriocephalus infection constituted 16% of total variability, which is in accordance with the data of other workers concerning the inheritance of some characters, such as resistance to invasive or infectious diseases (Kirpichnikov, 1979). In cases where parasite distribution was of the Poisson type, differences between different fish genotypes with respect to infection were not significant, but in October, when the parasite distribution was overdispersed, such differences became statistically significant. The increase of the effect of genotypic differences on the variability of fish with respect to Bothriocephalus infection towards the end of the season must be noted.

In 1985 differences in the infection were noted for two of the four loci investigated, but in 1986 only in one case of the seven possible cases. This is explained by the fact that in the former case there was group crossing, and in the latter - individual crossings. This why in the first case genetic differences between fish with respect to susceptibility to cestode infection were revealed within the host population, and in the second case, on the whole, between individual crossings.

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